A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 99: 363–370 (2025)
DOI: 10.3897/neobiota.99.148521

Short Communication

Coelomic foreign bodies in wild-caught *Python* spp. in the Greater Everglades Ecosystem, Florida, USA

Gretchen E. Anderson[1], McKayla M. Spencer[2], Ray W. Snow[3], Andrea F. Currylow[1,4], Frank N. Ridgley[5], Bryan G. Falk[3,6], Amy A. Yackel Adams[7]

1 *U.S. Geological Survey, Fort Collins Science Center - South Florida Field Station in Everglades National Park, 40001 SR 9336, Homestead, FL 33034, USA*
2 *Florida Fish and Wildlife Conservation Commission, Gainesville, FL 32601, USA*
3 *National Park Service, Everglades National Park, Homestead, FL 33034, USA*
4 *Current address: Department of Biology and Marine Biology, University of North Carolina, Wilmington, NC 28402, USA*
5 *Zoo Miami, Conservation and Research Department, 12400 SW 152nd Street, Miami, FL 33177, USA*
6 *Current address: National Invasive Species Council, Department of the Interior, 1849 C Street NW, Washington, DC 20240, USA*
7 *U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526, USA*
Corresponding author: Gretchen E. Anderson (g.anderson7790@gmail.com)

Abstract

Burmese pythons (*Python molurus bivittatus*) and African rock pythons (*Python sebae*) have established invasive populations in southern Florida, severely disrupting local ecosystems. We analysed necropsy data from 2,179 pythons captured between 2006 and 2022, revealing nine cases of coelomic foreign bodies, primarily consisting of bird beaks, which presumably entered the coelom following gastrointestinal perforations during prey consumption. Despite the presence of foreign bodies, most examined pythons exhibited no obvious health issues. These findings indicate that the consumption of prey with sharp morphological features, such as wading birds, may not impede the pythons' survival or health significantly, thereby underscoring their adaptability as apex predators in the Greater Everglades Ecosystem.

Key words: Digestion, invasive species, perforation

OPEN ACCESS

Academic editor: Michael McKinney
Received: 2 February 2025
Accepted: 24 May 2025
Published: 11 July 2025

Citation: Anderson GE, Spencer MM, Snow RW, Currylow AF, Ridgley FN, Falk BG, Yackel Adams AA (2025) Coelomic foreign bodies in wild-caught *Python* spp. in the Greater Everglades Ecosystem, Florida, USA. NeoBiota 99: 363–370. https://doi.org/10.3897/neobiota.99.148521

Copyright: This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

Pythons, like many snakes, constrict and swallow prey items whole, including a variety of animals that are greater than their own body mass (Bhupathy et al. 2014; Bartoszek et al. 2018; Mukherjee et al. 2019; Currylow et al. 2023). Swallowing prey whole can be a dangerous undertaking. Hard, sharp or spiny morphological features of prey can damage and/or puncture the gastrointestinal (GI) tract and body wall. Numerous publications have reported snake mortalities linked to feeding events, including ones caused by punctures (reviewed in Kornilev et al. (2023)). In the genus *Python*, documented cases of mortality caused by puncture or rupturing of the digestive tract include feeding attempts on an American alligator (*Alligator mississippiensis*) (Snow et al. 2007), a Cape porcupine (*Hystrix africaeaustralis*) (LiveScience 2015) and Indian crested porcupines (*Hystrix indica*) (Bhupathy et al. 2014; Mukherjee et al. 2019).

Burmese pythons (*Python molurus bivittatus*) are widely distributed across southern Florida (Guzy et al. 2023), including in Everglades National Park and Big Cypress National Preserve (Snow et al. 2007; Willson et al. 2011; Reed et al. 2012; McCleery et al. 2015). Since their establishment in Florida in the

late 1990s through early 2000s (Guzy et al. 2023), they have had detrimental impacts on the local ecosystems and animal populations, preying on numerous native species whose populations are now in decline and acting as a vector for diseases spreading to native snake species (McCleery et al. 2015; Miller et al. 2018; Westfall et al. 2019; Miller et al. 2020; Guzy et al. 2023). African rock pythons (*Python sebae*) are also established in southern Florida, but are currently restricted to western Miami-Dade County. African rock pythons are expected to have similar negative impacts to the ecosystem in Florida and several native species have been found in their digestive tracts (Reed et al. 2010; Christina Romagosa, University of Florida, written comm. 2024).

Both Burmese pythons and African rock pythons feed on a wide variety of vertebrates in their native and invasive ranges (Luiselli et al. 2001; Reed and Rodda 2009; Guzy et al. 2023; Christina Romagosa, University of Florida, written comm. 2024). They are consummate generalists and opportunists, feeding on vertebrates of appropriate size. Prey in their native range are not well documented and our current understanding relies heavily on observations of the closely-related Indian rock python (*P. molurus*). Indian rock pythons in southeast Asia consume a wide variety of mammals, birds, reptiles and amphibians ranging in size from small rodents to fully grown deer and even leopards (Wall 1921; Smith 1943; Pope 1961; Whitaker 1978; Bhupathy and Vijayan 1989; Reed and Rodda 2009). In southern Florida, Burmese pythons appear to maintain this diverse diet, consuming mammals, birds and reptiles of varying sizes, spanning from rats to deer and alligators (Snow et al. 2007; Reed and Rodda 2009; Dove et al. 2011; Romagosa et al. 2023). African rock pythons in central and western Africa consume a variety of mammals, reptiles, and domesticated fowl (Luiselli et al. 2001). In southern Florida, African rock python digestive tracts have contained mammals and birds (Reed et al. 2010; Christina Romagosa, University of Florida, written comm. 2024).

The U.S. Geological Survey (USGS), the National Park Service (NPS) and the Florida Fish and Wildlife Conservation Commission (FWC) manage programmes to capture and humanely euthanise these two invasive python species within the Greater Everglades Ecosystem. To maximise the value of the removal efforts, many of the resulting specimens are subsequently necropsied to provide scientific samples and data, such as body size, reproductive status and digestive tract contents (McCollister et al. 2021; Anderson et al. 2022; Currylow et al. 2022; Evers et al. 2024).

We necropsied 2,179 Burmese pythons and six African rock pythons during 2006–2022. Of these, eight Burmese pythons (< 0.004%) and one African rock python (0.16%) had foreign objects within their coelomic cavities (Table 1). The coelomic cavity is a hollow, fluid-filled cavity in the body that contains and protects internal organs, including the digestive tract. Herein, we provide observational details of these nine cases (pythons A–I, Table 1).

In six cases, pythons were found to have partial bird bones (specifically most of a bird bill) present within the body wall and outside of the digestive tract (python A, B, C, D, E and G, Table 1). These bills were adjacent to or near the stomach, usually encapsulated, sometimes with gross signs of abscessation. Some of the bills were solidly intact, while others broke apart upon extraction. Some objects were nearly completely broken down and unidentifiable (Table 1, pythons F and H). The foreign objects found within the coelomic cavities of python F and python H appeared to be a sharp bone-like fragment and a small, fractured bone, respectively.

Table 1. Summary of invasive, wild-caught, necropsied pythons (ID) found with coelomic foreign bodies from 2006 through 2021 in the Greater Everglades Ecosystem, Florida USA. Burmese pythons (*Python molurus bivittatus*) abbreviated to *P. m. bivittatus*. African rock pythons (*Python sebae*) abbreviated to *P. sebae*. Mass measured in grams (g). Snout-vent length (SVL) measured in centimetres (cm). Brief description of each ectopic item removed during necropsy and associated figure number when available.

Species	ID	Year	Sex	Mass (g)	SVL (cm)	Ectopic Item	Photo
P. m. bivittatus	A	2006	Female	5240	203	Unidentified bird bill	-
P. m. bivittatus	B	2007	Female	7810	283	Adult Frigate Bird (*Fregata magnificens*) bill	Fig. 1A, Fig. 1B
P. m. bivittatus	C	2007	Male	8630	235	Adult Great Blue or White Heron (*Ardea Herodias*) bill	Fig. 1C
P. m. bivittatus	D	2008	Female	7120	220	Unidentified bird bill	-
P. m. bivittatus	E	2011	Male	8622	228	Unidentified bird bill	-
P. m. bivittatus	F	2018	Male	4314	211	Unknown	-
P. m. bivittatus	G	2020	Female	23000	253	Unidentified bird bill	-
P. m. bivittatus	H	2021	Male	5026	193	Unknown	-
P. sebae	I	2021	Female	3787	188	Unidentified bird skull and bill	Fig. 1D

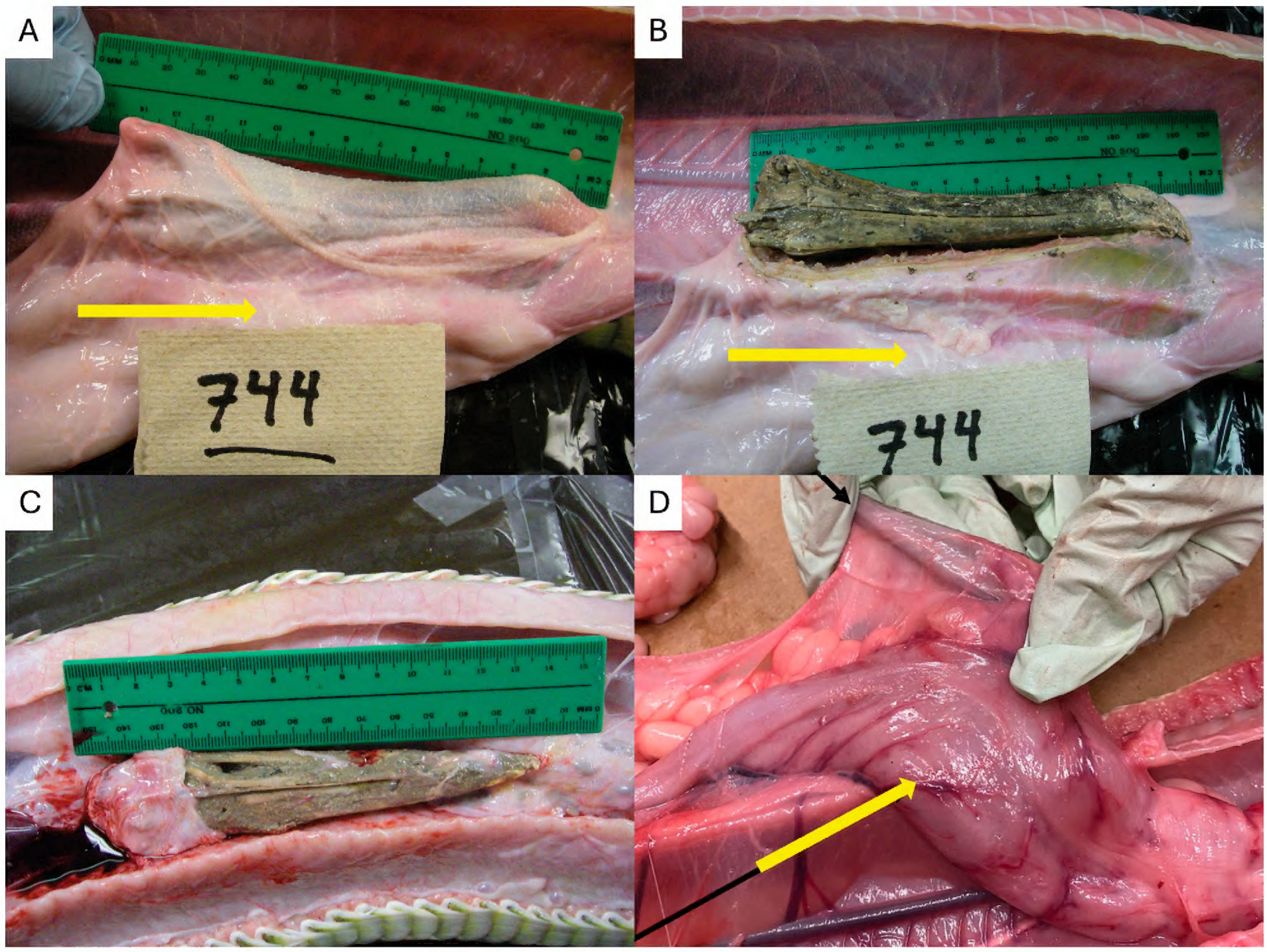

Figure 1. Selected photos of coelomic foreign bodies in necropsied pythons. Yellow arrows indicate the location of the stomach when visible. **A.** Coelomic foreign body visible outside the stomach of python B encased in body tissues; **B.** Same foreign body in python B, now identifiable as a bird bill, with encasing body tissues removed. **C.** Bird bill located outside the stomach of python C with encasing body tissues partially removed; **D.** Bird bill and skull located outside the stomach of python I fully encased in body tissues.

Python I contained a fully intact bird skull with intact bill (i.e. upper mandible fused and lower mandible still attached) outside of the gastrointestinal tract. Notably, in all cases, the stomachs were empty of any other digestive contents and showed no obvious gross signs of trauma or puncture. Although we cannot

determine the specific circumstances leading to the above-described foreign bodies' entry into the coelomic cavities, we presume that they originated from consumed prey items that punctured the digestive tract and then migrated into the coelom.

In seven of the nine cases, the python appeared to be in otherwise good health and showed no other internal gross abnormalities. However, python C exhibited internal irregularities including small, hard, multifocal grey/green nodules present in the mesentery near the stomach and extending throughout the liver parenchyma. In addition, python I had hard, multi-focal nodules throughout the liver parenchyma. Histopathology was not performed on these tissues to fully characterise the lesions, but they could be abscesses or granulomas associated with the perforation event.

It is unknown if these foreign bodies would have eventually caused negative health effects, nor could we determine how long the items had been within the coelomic cavities. Several foreign bodies appeared broken down and softened which could indicate that the items had been partially digested before puncturing the digestive tract or that the snake's immune system was beginning to break down the foreign material while encapsulated in the body cavity. As in most reptiles, snakes rely heavily on innate immune responses (Origgi 2007; Zimmerman et al. 2010). Innate immune responses are fast acting, facilitating reactions to threats within minutes to produce and circulate immune components such as antimicrobial peptides and phagocytes (Field et al. 2022). Antimicrobial proteins assist in preventing the spread of bacteria that may be present on the foreign bodies (van Hoek 2014), while phagocytes are capable of ingesting bacterial cells and other pathogens and breaking down other foreign materials (Origgi 2007). Given the potential severity of gastrointestinal perforation injuries from foreign bodies to other organisms, it is remarkable that these snakes are capable of enduring severe perforations without more obvious systemic illness. However, we acknowledge that snake mortalities due to GI punctures by foreign bodies are unlikely to be observed within our dataset as the majority of snakes in our set were captured alive or were carcasses collected alongside roads (presumed road strike mortalities).

Dietary analysis from wild caught invasive Burmese pythons documented 76 prey taxa, of which 48 were bird species or subspecies (Guzy et al. 2023; Romagosa et al. 2023). This includes wading birds with large, sharp bills (e.g. White Ibis [*Eudocimus albus*], Limpkin [*Aramus guarauna*] and American Bittern [*Botaurus lentiginosus*]). In the central Everglades, Burmese pythons may disproportionately occupy tree islands where there are dense bird rookeries, compared to islands that may have sparse mammal communities (Orzechowski et al. 2019 a, b). Our findings indicate that, in southern Florida, Burmese python consumption of whole wading birds with large, sharp or pointed bills may rarely seriously harm this species.

Burmese pythons have already been documented to have negative population-level impacts on native mammals in southern Florida (McCleery et al. 2015) with similar anticipated impacts for wading birds (Dove et al. 2011). Our observations underscore the dangers to wading birds, which serve as key indicator species for ongoing Greater Everglades Ecosystem restoration efforts (Doren et al. 2009). Further research would be useful to better understand adaptations these invasive and ecologically damaging constrictors have for healing gastrointestinal and body wall perforations, eliciting immune responses and encapsulating foreign bodies in the coelom.

Acknowledgements

We thank T.F. Dean, T. Pernas, M.F. McCollister and S. Schulze of the National Park Service (NPS) and N.G. Aumen of the U.S. Geological Survey (USGS) for facilitation of this project in Everglades National Park and Big Cypress National Preserve. We thank L. Addison, K. Scheiner, A. Schuhmann and anonymous reviewers for suggestions that improved the manuscript. We also thank A.L. Fitzgerald, C.J. Robinson, J.M. Josimovich and the many University of Florida research interns, NPS and USGS staff, volunteers, Florida Fish and Wildlife Conservation Commission (FWC) and South Florida Water Management District personnel that were involved with data collection. Some data were collected in association with activities conducted under NPS Scientific Research Permits BICY-00134 & -00159 and EVER-2018-SCI-0063, an interagency agreement between USGS and NPS #P18PG00352, FWC permits EXOT 19–43, -44, -45, and -114; EXOT 20–62, -63, -86, -93 and -184; and EXOT 21–71, -97, -111 and -278. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

All research was conducted under full compliance with federal and state legislation. No Institutional Animal Care and Use Committee approval was necessary because the invasive pythons were euthanized as part of mitigation management activities, but methods for safe euthanasia were developed in consultation with the NPS Wildlife Health Team.

Funding

Funding for the Everglades work and in-kind support was provided by the USGS Greater Ever-glades Priority Ecosystems Science (GEPES) Program, NPS and USGS Biothreats and Invasive Species Program.

Author contributions

Funding provision: Bryan G. Falk, Andrea F. Currylow, Amy A. Yackel Adams. Research conceptualization: Andrea F. Currylow, Gretchen E. Anderson, Amy A. Yackel Adams, McKayla M. Spencer. Data collection: Ray W. Snow, Bryan G. Falk, Andrea F. Currylow, Gretchen E. Anderson, McKayla M. Spencer. Data analysis: Andrea F. Currylow, Gretchen E. Anderson, McKayla M. Spencer. Subject expertise: Frank N. Ridgley. Writing original draft: Gretchen E. Anderson, McKayla M. Spencer, Amy A. Yackel Adams. Reviewing and editing: All authors contributed to improving the manuscript.

Author ORCIDs

Gretchen E. Anderson https://orcid.org/0000-0002-5887-4961
McKayla M. Spencer https://orcid.org/0000-0003-0001-4253
Andrea F. Currylow https://orcid.org/0000-0003-1631-8964
Frank N. Ridgley https://orcid.org/0000-0002-6819-2577
Bryan G. Falk https://orcid.org/0000-0002-9690-5626
Amy A. Yackel Adams https://orcid.org/0000-0002-7044-8447

Data availability

All of the data that support the findings of this study are available in the main text.

References

Anderson GE, Ridgley FN, Josimovich JM, Reed RN, Falk BG, Yackel Adams AA, Currylow AF (2022) Egg retention in wild-caught *Python bivittatus* in the Greater Everglades Ecosystem, Florida, USA. The Herpetological Journal 32(3): 109–113. https://doi.org/10.33256/32.3.109113

Bartoszek IA, Andreadis PT, Prokopervin C, Patel M, Reed RN (2018) *Python bivittatus* (Burmese python). Diet and prey size. Herpetological Review 49: 139–140.

Bhupathy S, Vijayan VS (1989) Status, distribution and general ecology of the Indian python *Python molurus molurus* Linn. in Keoladeo National Park, Bharatpur, Rajasthan. Journal of the Bombay Natural History Society 86: 381–387.

Bhupathy S, Ramesh C, Bahuguna A (2014) Feeding habits of Indian rock pythons in Keoladeo National Park, Bharatpur, India. The Herpetological Journal 24(1): 59–64.

Currylow AF, Falk BG, Yackel Adams AA, Romagosa CM, Josimovich JM, Rochford MR, Cherkiss MS, Nafus MG, Hart KM, Mazzotti FJ, Snow RW, Reed RN (2022) Size distribution and reproductive phenology of the invasive Burmese python (*Python molurus bivittatus*) in the Greater Everglades Ecosystem, Florida, USA. NeoBiota 78: 129–158. https://doi.org/10.3897/neobiota.78.93788

Currylow AF, Fitzgerald AL, Goetz MTH, Draxler JL, Anderson GE, McCollister MF, Romagosa CM, Yackel Adams AA (2023) Natives bite back: Depredation and mortality of invasive juvenile Burmese pythons (*Python bivittatus*) in the Greater Everglades Ecosystem. Management of Biological Invasions 14(1): 107–122. https://doi.org/10.3391/mbi.2023.14.1.06

Doren RF, Trexler JC, Gottlieb AD, Harwell MC (2009) Ecological indicators for system-wide assessment of the greater everglades ecosystem restoration program. Ecological Indicators 9(6): S2–S16. https://doi.org/10.1016/j.ecolind.2008.08.009

Dove CJ, Snow RW, Rochford MR, Mazzotti FJ (2011) Birds consumed by the invasive Burmese python (*Python molurus bivittatus*) in Everglades National Park, Florida, USA. The Wilson Journal of Ornithology 123(1): 126–131. https://doi.org/10.1676/10-092.1

Evers TM, Currylow AF, Sandfoss MR, McBride LM, Romagosa CM, Boone WW, Guzy JC, Anderson GE, Hart KM, McChollister MF, Yackel Adams AA (2024) Double Take: Ingestion of two rats by a juvenile Burmese Python (*Python bivittatus)* in Big Cypress National Preserve, Florida, USA. Reptiles & Amphibians : Conservation and Natural History 31(1): e21283. https://doi.org/10.17161/randa.v31i1.21283

Field EK, Hartzheim A, Terry J, Dawson G, Haydt N, Neuman-Lee LA (2022) Reptilian innate immunology and ecoimmunology: What do we know and where are we going? Integrative and Comparative Biology 62(6): 1557–1571. https://doi.org/10.1093/icb/icac116

Guzy JC, Falk BG, Smith BJ, Willson JD, Reed RN, Aumen NG, Avery ML, Bartoszek IA, Campbell E, Cherkiss MS, Claunch NM, Currylow AF, Dean T, Dixon J, Engeman R, Funck S, Gibble R, Hengstebeck KC, Humphrey JS, Hunter ME, Josimovich JM, Ketterlin J, Kirkland M, Mazzotti FJ, McCleery R, Miller MA, McCollister MF, Parker M, Pittman M, Rochford SE, Romagosa M, Roybal CM, Snow A, Spencer RW, Waddle MM, Yackel JH, Adams AA, Hart KM (2023) Burmese pythons in Florida: A synthesis of biology impacts and management tools. NeoBiota 80: 1–119. https://doi.org/10.3897/neobiota.80.90439

Kornilev YV, Natchev ND, Lillywhite HB (2023) Perils of ingesting harmful prey by advanced snakes. Biological Reviews of the Cambridge Philosophical Society 98(1): 263–283. https://doi.org/10.1111/brv.12906

LiveScience (2015) Python Eats Porcupine, Regrets It Later (Here's Why). https://www.livescience.com/51364-python-eats-porcupine.html

Luiselli L, Angelici FM, Akani GC (2001) Food habits of *Python sebae* in suburban and natural habitats. African Journal of Ecology 39(1): 116–118. https://doi.org/10.1111/j.1365-2028.2001.00269.x

McCleery RA, Sovie A, Reed RN, Cunningham MW, Hunter ME, Hart KM (2015) Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. Proceedings. Biological Sciences 282: 1–7. https://doi.org/10.1098/rspb.2015.0120

McCollister MF, Josimovich JM, Fitzgerald AL, Jansen DK, Currylow AF (2021) Native mammalian predators can depredate adult Burmese pythons in Florida. Southeastern Naturalist 20(2): N55–N99. https://doi.org/10.1656/058.020.0205

Miller MA, Kinsella JM, Snow RW, Hayes MM, Falk BG, Reed RN, Mazzotti FJ, Guyer C, Romagosa CM (2018) Parasite spillover: Indirect effects of invasive Burmese pythons. Ecology and Evolution 8(2): 830–840. https://doi.org/10.1002/ece3.3557

Miller MA, Kinsella JM, Snow RW, Falk BG, Reed RN, Goetz SM, Mazzotti FJ, Guyer C, Romagosa CM (2020) Highly competent native snake hosts extend the range of an introduced parasite beyond its invasive Burmese python host. Ecosphere 11(16): e03153. https://doi.org/10.1002/ecs2.3153

Mukherjee A, Pal A, Velankar AD, Kumara HN, Bhupathy S (2019) Stay awhile in my burrow! Interspecific associations of vertebrates to Indian crested porcupine burrows. Ethology Ecology and Evolution 31: 313–328. https://doi.org/10.1002/ecs2.3153

Origgi F (2007) Reptile immunology. In: Jacobson ER (Ed.) Infectious diseases and pathology of reptiles. Taylor and Francis, New York, 131–166. https://doi.org/10.1201/9781420004038.ch2

Orzechowski SCM, Frederick PC, Dorazio RM, Hunter ME (2019a) Environmental DNA sampling reveals high occupancy rates of invasive Burmese pythons at wading bird breeding aggregations in the central Everglades. PLoS ONE 14(4): e0213943. https://doi.org/10.1371/journal.pone.0213943

Orzechowski SCM, Romagosa CM, Frederick PC (2019b) Invasive Burmese pythons (Python bivittatus) are novel nest predators in wading bird colonies of the Florida Everglades. Biological Invasions 21: 2333–2344. https://doi.org/10.1007/s10530-019-01979-x

Pope CH (1961) The giant snakes. Alfred A. Knopf, New York.

Reed RN, Rodda GH (2009) Giant Constrictors: Biological and Management Profiles and an Establishment Risk Assessment for Nine Large Species of Pythons, Anacondas, and the Boa Constrictor. U.S. Geological Survey Open-File Report, 2009–1202. https://doi.org/10.3133/ofr20091202

Reed RN, Krysko KL, Snow RW, Rodda GH (2010) Is the Northern African python (*Python sebae*) established in southern Florida? Reptiles & Amphibians : Conservation and Natural History 17(1): 52–54. https://doi.org/10.17161/randa.v17i1.16069

Reed RN, Willson JD, Rodda GH, Dorcas ME (2012) Ecological correlates of invasion impact for Burmese pythons in Florida. Integrative Zoology 7: 254–270. https://doi.org/10.1111/j.1749-4877.2012.00304.x

Romagosa CM, Mazzotti FJ, Snow RW, Bartoszek I, Dove CJ, Juárez-Sánchez AD, Suarez E, Rochford MR, Krysko KL, Cherkiss MS, Falk BG, Josimovich JM, Yackel Adams AA, Currylow AF, Hart KM, Reed RN (2023) Diet of invasive Burmese Pythons (*Python molurus bivittatus*) in southern Florida, 1995–2020. U.S. Geological Survey data release. https://doi.org/10.5066/P9A0V89V

Smith MA (1943) The Fauna of British India, Ceylon and Burma including the whole of the Indo-Chinese Sub-region, Reptilia and Amphibia Vol. III, Serpents. Taylor and Francis, London.

Snow RW, Krysko KL, Enge KM, Oberhofer L, Warren-Bradley A, Wilkins L (2007) Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in Southern Florida. In: Henderson RW, Powell R (Eds) Biology of the Boas and Pythons. Eagle Mountain Publishing, Utah, 365–386.

Van Hoek ML (2014) Antimicrobial peptides in reptiles. Pharmaceuticals 7(6): 723–753. https://doi.org/10.3390/ph7060723

Wall F (1921) Ophidia Taprobanica: Or, The Snakes of Ceylon. Government printer, Sri Lanka. https://doi.org/10.5962/bhl.title.53694

Westfall AK, Miller MA, Murray CM, Falk BG, Guyer C, Romagosa CM (2019) Host-specific phenotypic variation of a parasite co-introduced with invasive Burmese pythons. PLoS ONE 14(1): e0209252. https://doi.org/10.1371/journal.pone.0209252

Whitaker R (1978) Common Indian snakes. A field guide. Macmillan India Limited, Delhi.

Willson JD, Dorcas ME, Snow RW (2011) Identifying plausible scenarios for the establishment of invasive Burmese pythons (*Python molurus*) in southern Florida. Biological Invasions 13: 1493–1504. https://doi.org/10.1007/s10530-010-9908-3

Zimmerman LM, Vogel LA, Bowden RM (2010) Understanding the vertebrate immune system: Insights from a reptilian perspective. The Journal of Experimental Biology 213: 661–671. https://doi.org/10.1242/jeb.038315